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FOOD UPTAKE, GROWTH AND SURVIVAL OF CAPELIN LARVAE *(MALLOTUS VILLOSUS* Müller) IN AN OUTDOOR CONSTRUCTED BASIN

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ABSTRACT

MOKSNESS, E. 1982. Food uptake, growth and survival of capelin larvae *(Mallotus villosus* Müller) in an outdoor constructed basin. *Fisk Dir. Skr. Ser. HavUnders.*, *17*: 267–285.

An experiment with a population of capelin larvae was carried out in an outdoor basin of 2000 m^3 in 1979. Data on food uptake, growth and survival of capelin larvae were collected over a period of 127 days.

The first sample from the basin showed that some larvae had been feeding at an age of 5 days. Under the same temperature conditions (8°C), the capelin larvae, kept in the laboratory, started to feed at age 4 days. Sea-caught larvae from 1971 had started to feed at the same development stage as in the laboratory experiment.

The basin experiment indicated that capelin larvae fed upon the most dominant organism of an appropriate size: the larvae of *Spionidae* spp. for the first 60 days and the veligers of *Littorina* spp. for the last 60 days. Partial or total defecation of the gut content made it impossible to calculate the daily food uptake.

The capelin larvae in the basin had their maximum increase in length a few days after the end of the yolk sac stage (EYS), (0.29 mm/day), decreasing slowly to 0.20 mm/day, giving a total specific growth rate of 4.1%. Similar growth was not observed in the feeding group in the laboratory. The length-weight relationship for the basin and the sea-caught larvae was nearly the same.

The mass mortality period (age 20–40 days) of the capelin larvae in the basin experiment was delayed and prolonged compared to mass mortality (age 14–22 days) of the starving group in the laboratory. The results from the sea-caught larvae indicated a similar mass mortality as in the basin experiment.

The basin experiment gave 2.1% survival of the capelin larvae over a period of 127 days.

INTRODUCTION

In order to interpret field observations, LASKER (1975) carried out laboratory experiments on growth and mortality of fish larvae at known food supplies. MAY (1974) pointed out the difficulties of interpreting laboratory experiments with direct field observations due to a large number of independent variables influencing the population dynamics of larval fish. Alternative approaches to obtain a better understanding of survival, growth and food uptake of fish larvae are desired.

The use of a large enclosed volume of water in the study of larval fish population dynamics was recommended by HUNTER (1976). The development of such enclosed systems in the study of fish larvae in recent years is discussed by SOLEMDAL (in press).

The present article gives the main results of survival, growth and food uptake experiments with capelin larvae in 1979, using a large basin which contained self-sustaining natural populations of phyto- and zooplankton. No known predators on capelin larvae were present in the basin. A known number of known-age capelin larvae were present in the basin at the beginning and end of the experiment. Simultaneous laboratory experiments with capelin larvae indicated when the feeding started and the time of mass mortality of capelin larvae caused by starving. The results are compared with field observations in 1971 on capelin larvae from the Barents Sea stock.

The experiment were carried out at the State Biological Station Flødevigen, near Arendal in southern Norway.

MATERIALS AND METHODS

Eggs naturally spawned by Barents Sea capelin at 24 m depth and 1.7°C near Kibergneset, in Finnmark, northern Norway, were transported to the station and incubated in the laboratory at a temperature of 5±0.5°C. Larval age and the experimental period are reported in days from 16 May, the date for 50% hatching. The hatching started on 14 May.

All the samples were preserved immediately after capture, in 4% buffered formaldehyde in sea water. All capelin larvae were examined for gut content and dry weight.

The gut contents were identified and the mean number of prey organisms per larvae was calculated. Larvae of *Spionidae* spp. and unidentified matter were impossible to count and are given in terms of the percent of capelin larvae containing this material. Unidentified matter consisted mainly of various phytoplankton organisms and the remains of copepods.

The specific growth rate (SHELBOURNE *et al.* 1973)

$$SGR = (\ln DW_n - \ln DW_0)/(t_n - t_0)$$

where DW_n = dry weight at day n, and the growth in length was calculated from dry weight and standard length on the day of 50% hatching (t_0), respectively.

The yolk sac volume (YV) has been calculated according to the formula

$$YV = 4/3\ YL\ YH^2$$

as described in HELGESEN (1977). YL = yolk sac length and YH = yolk sac height.

LABORATORY EXPERIMENTS

Experiments with starving capelin larvae were carried out by placing 100 newly hatched capelin larvae in each of eight 8 l clear plexiglass cylinders (DANIELSSEN og IVERSEN 1974) containing stagnant water.

One cylinder was emptied and examined every other day, the first at a larval age of 9 days. The mortality curve for starving larvae was established from these experiments. Feeding experiments were carried out by placing about 1000 newly hatched capelin larvae in each of two 50 l black cylindrical aquaria (DANNEVIG og HANSEN 1952).

Zooplankton prey organisms were collected every day from Flødevigen Bay and consisted mainly of adults, copepodits and nauplii of calanoid copepods, unidentified rotifers and larvae of *Spionidae* spp. Collections were made with plankton nets fitted with 90 µm mesh size, and were sieved through a net with 500 µm mesh size in the laboratory. Each day 40 larvae were collected from the feeding group and preserved after being fed for 5 hours. The temperature was increased from 6.0°C at the beginning to 8°C at the end of all the experiment.

BASIN EXPERIMENTS

The basin had a volume of 2000 m^3, a surface area of 660 m^2 and a maximum depth of 5 m. Fig. 1 shows a sketch of the basin.

The basin was supplied with water taken through a reservoir from a depth of 75 m. The water exchange was 2–3% per day. The water was introduced at the bottom. A stable level was maintained by a run-off pipe at the surface equipped with 500 µm filter. Measurements of salinity, temperature and oxygen saturation, were made out once a week at the following depths: 0, ½, 1, 2, 3, 4 and 5 m (bottom) at staton A (Fig. 1).

Zooplankton was collected mainly with an electrical pump with a capacity of 70 litres per minute. The pumping time was 30 sec. and the pumped water was filtered through a 90 µm size net. Samples were taken from 7 depth strata at station A and from 5 depth strata at station B. These strata were 0, ½, 1, 2, 3, 4 m depth and 10 cm above the bottom at station A and 0, ½, 1, 2 m depth and 10 cm above the bottom at station B. The strata at station A represent 175, 325, 490, 530, 360, 100 and 20 m^3. Hence the total volume of the basin is 2000 m^3. The overall mean density of zooplankton in the basin was calculated by weighting the density at each strata by the volume of that strata.

No corrections are made for avoidance or other causes of underestimating plankton densities.

Approximately 100,000 capelin larvae, estimated to within 10%, were transferred to the basin on 19 May, at age 3 days. The capelin larvae were sampled horizontally at 0, 1, 2 and 3 m at 0900, 1500 and 2400 hours, except for the period after 24 July (64 days) when samples were taken only at 2400 hours.

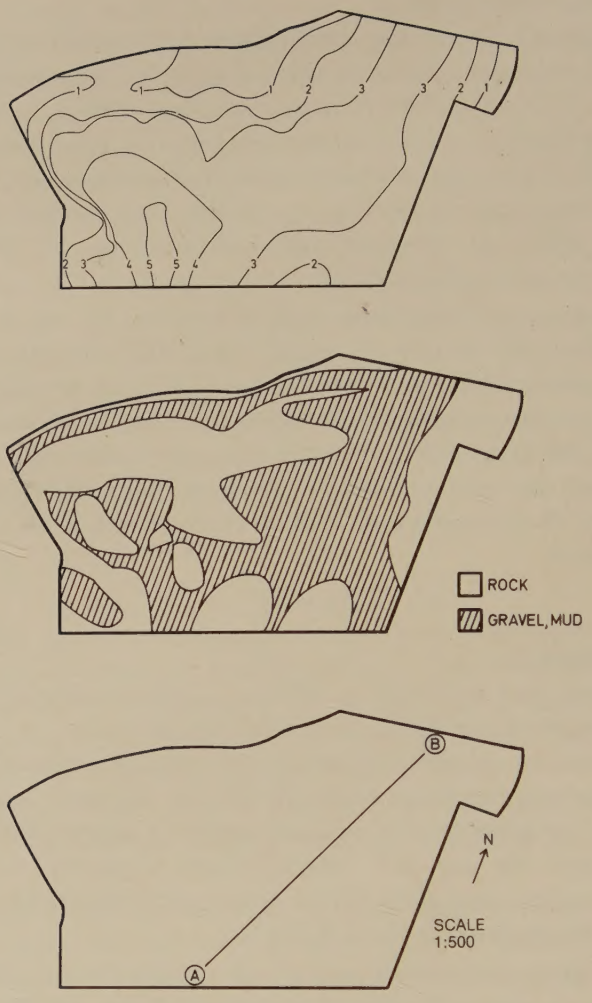

Fig. 1. A plan of the basin showing the depth contours (top), the different bottom substrates (middle), and the position of the hydrographical station A, the pumping stations A and B and the net haul from A to B (bottom).

The two-chamber nets (ELLERTSEN *et al.*, in press) used in the collections of capelin larvae were fitted with 350 μm and 500 μm mesh: the first was used up to an age of 16 days and the other, for the rest of the experimental period. The nets were hauled with a speed of 0.4 m/s. In order to estimate the number of capelin larvae at any time in the volume of the basin where larvae were sampled, the number caught per cubic meter water filtered at each depth, assuming ideal filtration, is multiplied by the volumes of water allocated to that depth. The allocated volumes were 640, 530 and 360 m^3 for 1, 2 and 3 m depths, respectively. The basin was drained on 20 September when the capelin larvae were 127 days old.

FIELD SURVEYS

The coast off Troms and Finnmark (67°N 11°E to 79°N 38°E) was surveyed for capelin larvae in May and June 1971 (SLINNING 1976). Samples were taken in the upper 75 m with Clarke-Bumpus plankton samplers with a mesh size of 500 µm. Capelin larvae from 46 different stations have been examined. The towing speed was 0.8–1.0 m/s. The temperature and salinity in the surveyed area, down to 75 m, were between 3–8°C and 33–34‰.

RESULTS

HYDROGRAPHY

The isotherms in the basin during the experimental period are indicated in Fig. 2. The temperature increased from 6 to 13°C at the bottom and reached a maximum of 20°C at the surface. A thermocline was established between 1.5–2.0 m for most of the experimental period.

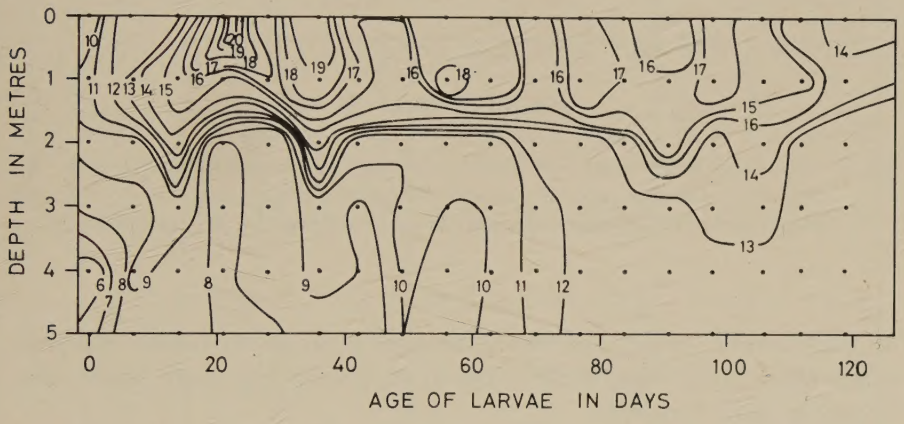

Fig. 2. The isotherms in the basin during the experimental period.

The salinity was between 32–34‰ and the oxygen saturation from 100–150%, except for a short period around 90 days when it was near 40% at the bottom.

PHYTO- AND ZOOPLANKTON

The concentration of chlorophyll *a* varied between 2–7.5 mg/m^3 in the basin during the experimental period.

Fig. 3 gives the mean number of different food items in the basin. It shows that larvae of *Spionidae* spp. dominated in the zooplankton during the first 60 days (10 organisms/1), while veligers of *Littorina* spp. dominated for the rest of the experimental period (5 organisms/1). Table 1 gives the vertical densities of copepod nauplii, larvae of *Spionidae* spp. and veligers of *Littorina* spp. during

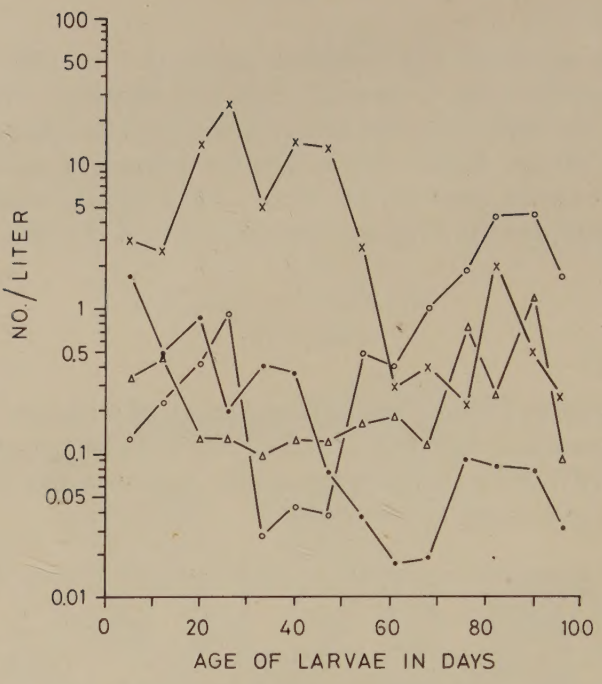

Fig. 3 The overall mean density per liter in the basin of copecod nauplii (•———•), veligers of *Littorina* spp. (o———o), larvae of *Spionidae* spp. (x———x) and harpacticoid and calanoid copecods (△———△) from 16. May onwards.

the experimental period. The highest densities of larvae of *Spionidae* spp. were found below 3 m depth, while veligers of *Littorina* spp. were found most frequently above 3 m depth.

The length of veligers of *Littorina* spp. varied from 120 to 300 μm, while larvae of *Spionidae* spp. varied from 360 to 1860 μm with an average length of 700 μm throughout the experimental period.

FOOD UPTAKE

The length of the smallest and longest prey organisms found in the gut of capelin larvae from the basin experiment are shown in Fig. 4. The length of the longest prey organisms increased from 300 to 1230 μm at a larval length from 7 to 20 mm. Up to a larval length of 40 mm the figure indicates a lesser increase to 1400 μm of the prey organisms. The smallest prey organiss found in the guts of larvae from most of the experimental period consisted mainly of unidentified flagellates (40–50 μm) and *Exuviaella* cf. *baltica* (9–15 μm), and some *Proto peridinium* spp. (16–36 μm) and *Nitzschia closterium* (40–50 μm). Very little of the unidentified matter seemed to be digested. Larvae of *Spionidae* spp. found in the gut were impossible to measure.

Table 1. Densities in number per litre (a) copepod nauplii, (b) larvae of Spionidae spp. and (c) veliger of Littorina sp. in the basin during the experimental period.

	Depth in m.	Date												
		21/5	28/5	5/6	11/6	18/6	25/6	2/7	9/7	16/7	23/7	31/7	6/8	14/8	20/8
	0	0.8	0.5	+	0.2	0.1	0.1	0.1	0	0	0	0.1	0.2	0.2	+
	0.5	0.5	0.4	1.0	0	0.2	+	0	+	0	+	+	0.1	0.1	0
	1	1.1	0.6	1.1	0.2	+	0.2	0.1	0	0	+	0.1	0.1	0.1	+
a)	2	1.7	0.7	0.4	0.1	0	0	0	0	0	0	0.1	+	0.1	+
	3	3.7	0.3	0.9	+	0	0	+	0	0	0	+	0.1	+	+
	4		0.4	0.5	0.6	0.1	+	+	+	0	0	0	0	0	0.1
	a.b.++	2.5	0.8	2.2	0.5	1.1	1.9	0.3	0.2	0.1	0.1	0.5	0.2	0.1	0.1
	0	+	0.1	0.1	1.8	0.4	0.1	1.0	0.2	0.1	0.1	0.2	0.1	0.1	+
	0.5	0.1	0.2	0.1	0.2	0.1	0.2	0.2	+	0.1	+	0.2	0.1	+	0.2
	1	0.1	0.1	+	+	0.1	+	0.1	0.1	0.1	0.2	+	0.1	0.1	0.1
b)	2	0.6	6.0	0.1	0.4	2.7	0.1	0.2	3.4	0.3	0.1	0.1	0.2	1.7	0.1
	3	0.6	6.0	0.1	0.4	2.7	0.1	0.2	3.4	0.3	0.1	0.1	0.2	1.7	0.1
	3	+	0.5	1.0	2.2	0	1.0	+	0.3	0.2	0.2	0.1	+	0.1	0
	4		2.6	44.7	124.2	7.6	15.8	9.6	1.6	0.1	0.8	0.1	13.6	0.2	+
	a.b.++	14.0	7.7	48.3	54.0	25.8	83.5	82.0	14.0	1.4	1.7	0.9	1.1	1.6	1.0
	0	0.1	0.2	0.9	0.2	+	+	+	0.2	1.3	0.7	0.2	2.3	2.5	1.2
	0.5	0.3	0.5	0.5	2.0	+	0	+	0.7	0.7	2.6	4.1	8.5	5.7	1.2
	1	0.1	0.2	0.8	0.1	0.1	0	+	1.9	0.3	3.0	5.9	5.7	15.1	3.7
c)	2	0.2	0.3	0.1	0.3	0	+	+	+	+	+	0.2	10.5	7.6	0.5
	3	+	0.2	0.1	0.8		0.2	0	0	0.5	0.1	0.1	0.9	1.8	0.3
	4		0.1	0.6	0	+	+	0	0	2.6	3.0	0	4.1		
	a.b.++	0.1	0.3	0.1	0	0.1	0.1	0.2	0.7	0.2	0.6	0.8	1.7	1.2	1.3

+) Density greater than 0, less than 0.1.

++) 10 cm above the bottom.

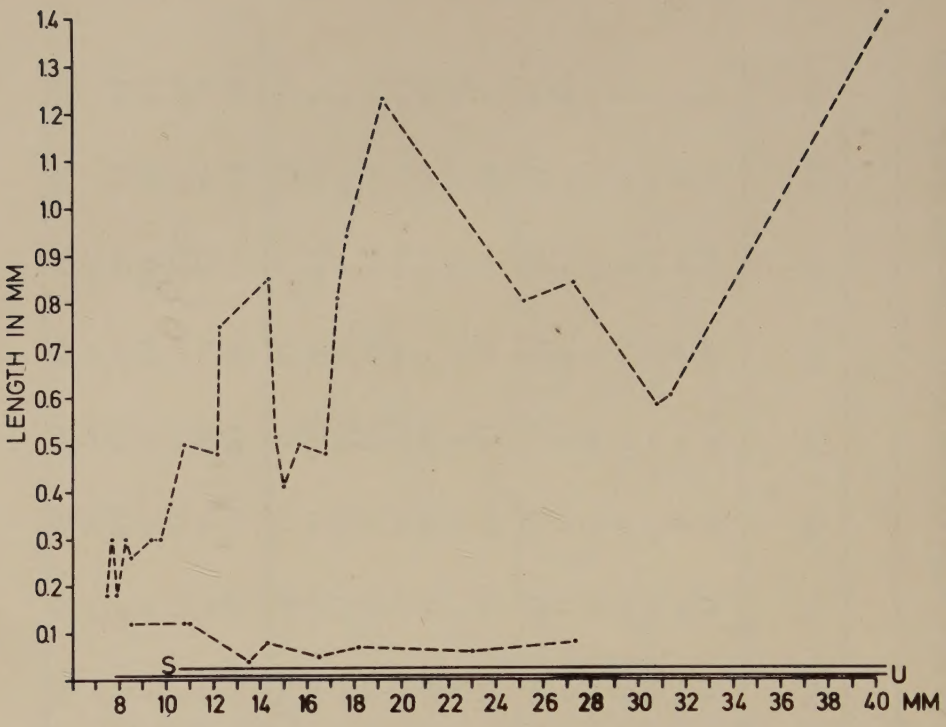

Fig. 4. The longest and smallest prey organism ingested at a given larval length in the basin experiment. S = larvae of *Spioniadae* spp. found in the gut, U = unidentified matter found in the gut.

Tables 2 and 3 show the different food items in the gut of capelin larvae from the basin and field, respectively. Larvae of *Spionidae* spp. and unidentified matter dominated in the gut of capelin larvae from the basin during the first 60 days, while veligers of *Littorina* spp. dominated for the rest of the experimental period. Calanoid copepods were found frequently in the gut during the whole period. After the decrease of *Spionidae* spp. in the gut content, the mean number of organisms/larvae increased more than 30 times. In the gut of capelin larvae from the field, the number of food items was at the same level as in the basin and no particular prey group dominated. Unidentified matter was found in an increasing number of larvae longer than 13 mm.

Table 2. Gut content of capelin larvae from the basin experiment given as mean number og organisms per larvae with gut content. Larvae of *Spionidae* spp. and unidentified matter are given in percent. The highest number is underlined.

Capelin larvae		Mean number of different food items per larvae					Percentage of larvae with:	
Age in days	No.	Total	Copepod nauplii	Harpacticoid and Calanoid copepods	Veligers of Littorina spp.	Others	Unidentified matter	Larvae of Spionidae spp.
5	27						4	
6	19							
7	34	2.80	1.30			*1.50*		
8	40							
9	45	0.90		0.20	0.20	*0.50*		
10	21	2.00			1.00	1.00	5	
11	22	1.00		*1.00*				
12	99	0.80	0.20	*0.40*		0.20	2	
15	38						3	
16	145	1.60		0.30		*1.30*	1	1
20	136	0.20		0.10		0,10	11	8
23	121	0.40	0.20			0.20	14	13
26	145	0.06		0.02		*0.04*	32	35
29	148	0.03		*0.03*			22	20
33	64	0.31	0.05	*0.14*		0.12	30	13
35	71	0.06		0.03		0.03	38	30
40	48	0.21	0.05	*0.11*		0.05	25	21
41	15	0.70		0.20		*0.50*	60	7
43	68	0.44		*0.38*		0.06	22	34
47	78	1.53	0.11	0.26		*1.16*	31	64
50	110	1.44	0.31	0.16	0.05	*0.92*	43	44
54	40	0.22		*0.22*			15	15
57	40	0.56	0.07	*0.49*			40	23
64	40	6.16	*3.95*	0.37	1.84		50	25
68	16	30.04	0.38	0.26	*29.40*			19
71	20	49.93		1.00	*48.93*		60	5
75	14	28.98	10.14	1.00	*16.42*	1.42	14	
78	31	18.34	0.28	3.24	*14.60*	0.22	13	7
82	26	58.47	15.79	1.11	*35.10*	6.47	8	15
85	22	18.04		1.29	*16.50*	0.25	18	
89	5							
92	17							
96	31							
99	22	0.32		0.16		0.16	18	9
115	20	26.51	0.13	3.13	6.25	*17.00*	5	20
117	20	3.17	0.17	*2.92*	0.08			5
127	27	0.30		*0.30*			37	

Table 3. Gut content of capelin larvae from the sea in 1971 given as mean number of organisms per larvae with gut content with a) decreasing yolk sac volume, and b) increasing standard length after yolk sac stage. The highest number is underlined.

Capelin larvae		Mean number of different food items per larvae				Percentage of larvae with unidentified matter
Yolc sac volume ($mm^3 \cdot 10^{+3}$)	Number	Total	Copepod naulii	Harpactiocid and calanoid copepods	Others	
30	61					
29–30	26	2.00	1.00	1.00		
19–10	42	1.80	0.42	*1.00*	0.42	
9– 0	260	0.75	*0.41*	0.27	0.07	5

b)

Capelin larvae		Mean number of different food items per larvae				Percentage of larvae with unidentified matter
Standard length groups (mm)	Number	Total	Copepod naplii	Harpacticoid and Calanoid copepods	Others	
6.0– 6.4	8					
6.5– 6.9	8					
7.0– 7.4	33	1.00		*1.00*		
7.5– 7.9	55	0.74	0.37	0.37		2
8.0– 8.4	75	0.63	*0.63*			3
8.5– 8.9	89	0.15			*0.15*	8
9.0– 9.4	129	1.04		0.52	0.52	3
9.5– 9.9	89	0.18		*0.18*		7
10.0–10.4	84					6
10.5–10.9	58	0.44			*0.44*	7
11.0–11.4	36					3
11.5–11.9	31					7
12.0–12.4	20					5
12.5–12.9	20					5
13.0–13.4	11					18
13.5–13.9	8					13
14.0–14.4	9					33
14.5–14.9	7					14

FEEDING INCIDENCE

Fig. 5 shows the feeding incidence and the decrease of yolk sac volume of the capelin larvae in the laboratory feeding groups. The larvae started feeding at 4 days of age, the yolk sac volume being 0.020 mm^3. An average feeding incidence of 25% was observed. The mean number of prey organisms in the gut of the larvae was about 2–3. However, all of these larvae, like those in the starved group, also died within 22 days. Until the end of the yolk sac stage (EYS) the larvae had a growth in length of 0.06 mm/day.

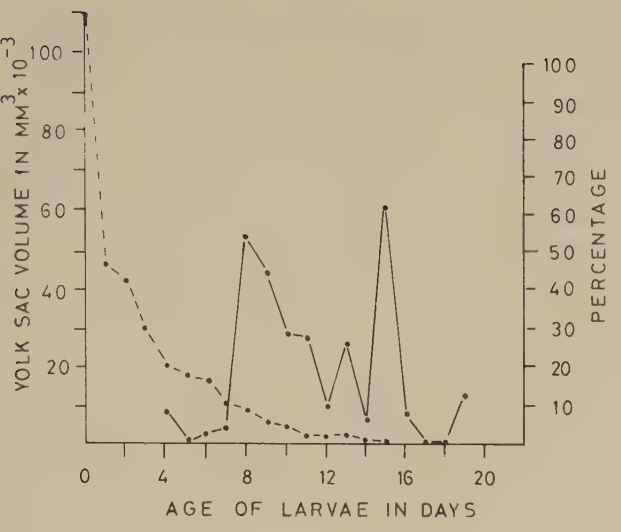

Fig. 5. The feeding incidence of the capelin larvae (———) from the laboratory experiment. The decrease in yolk sac volume (– – – –) is indicated. (N = 654).

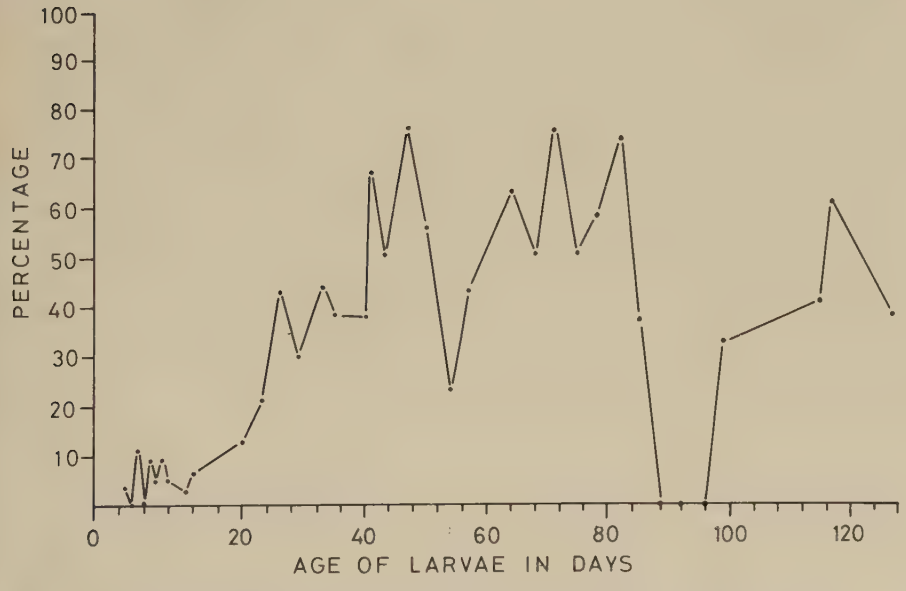

Fig. 6. The feeding incidence of capelin larvae from the basin (N = 1833).

The feeding incidence of capelin larvae in the basin are given in Fig. 6. When sampling started on day 5, the larvae had started feeding. The feeding incidence was below 10% until day 25 and then increased to 70% at day 40.

Feeding incidence of capelin larvae from the field in 1971 is shown in Fig. 7. Feeding started at a yolk sac volume of 0.025 mm^3, the feeding incidence having an average of 6% up to a larval length of 13–14 mm and increasing after this length was reached.

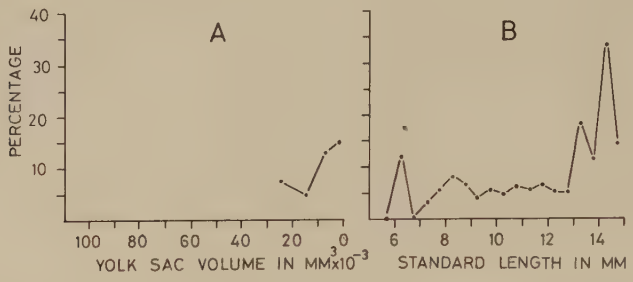

Fig. 7. The feeding incidence of capelin larvae from the field in 1971 with a) larvae with yolk sac and b) larvae without yolk sac. (N = 1160).

GROWTH

Fig. 8 gives the mean length of the capelin larvae in the basin. Mean growth during the first 12 days was calculated to be 0.29 mm/day. After that, growth decreased and was about 0.20 mm/day from age 40 days until termination of the experiment. The specific growth rate (SGR) for the whole period was 4.1%. Capelin larvae from the basin, aged 25 days, were about 13 mm.

Fig. 9 shows the length distribution of capelin larvae from the field in 1971 and from the basin experiment in 1979. Mostly capelin larvae below 15 mm in length were caught in the field surveys. The length-weight relationships of the capelin larvae from the field in 1971 and the basin in 1979, up to a length of 15 mm, were $DW = 0.00036\ SL^{2.5969}$ (r^2=0.94) and $DW = 0.00029\text{-}SL^{2.6836}$ (r^2=0.96), respectively.

SURVIVAL

The mass mortality of starving larvae in the laboratory took place between day 14 and 18. The last one died on day 22.

The mean number of capelin larvae per cubic meter caught within 1, 2 and 3 m depths in the basin at 0900, 1500 and 2400 hours are given in Fig. 10. The catch curves show that a greater number of larvae were caught at nighttime than at daytime. Table 4, which shows the number of larvae caught per cubic meter in 1, 2 and 3 m depths at 0900, 1500 and 2400 hours, indicates that the larvae were closer to the bottom of the basin at daytime than at nighttime. At 2400 hour most of the larval were taken at 2 and 3 m depths, except for the

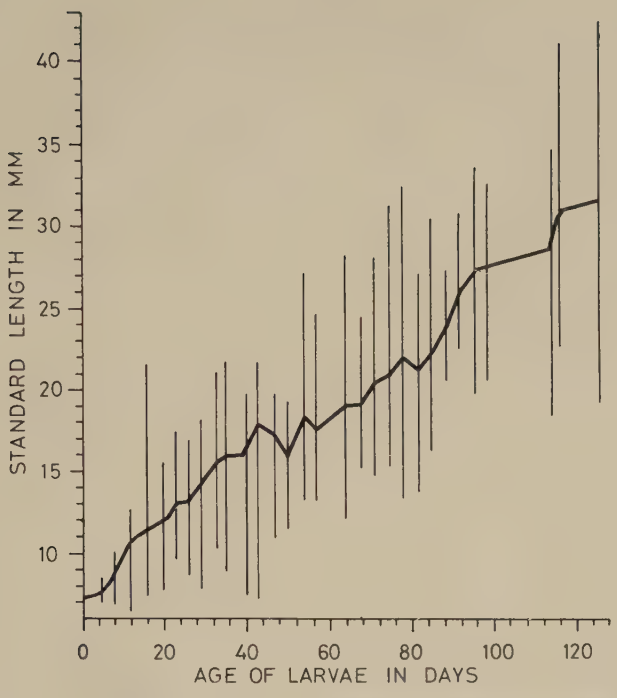

Fig. 8. Mean length of capelin larvae from the basin. Vertical bars = range. (N = 10257).

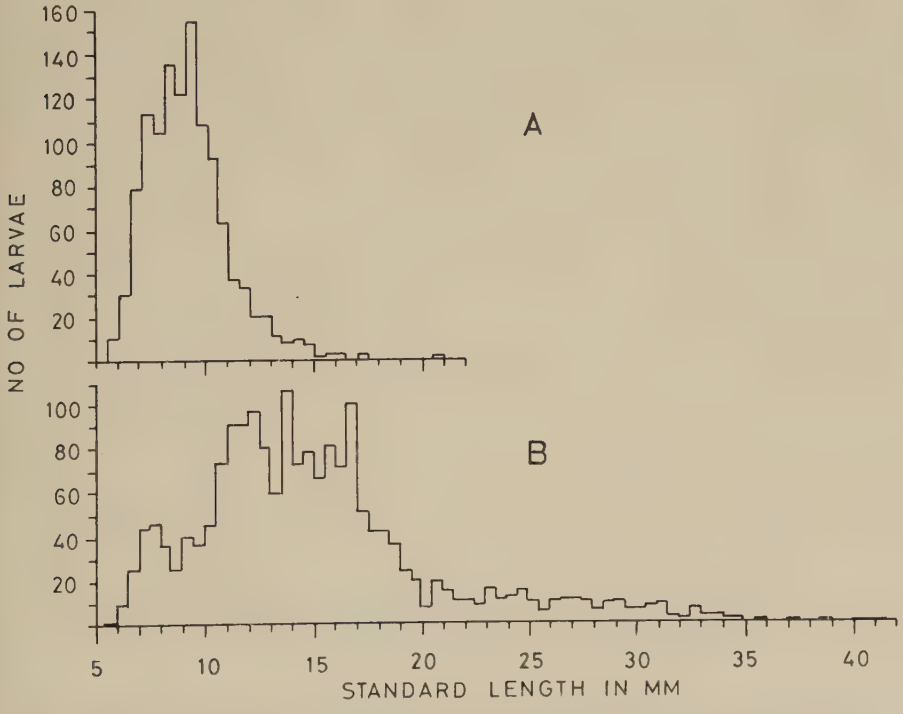

Fig. 9. The length distribution of capelin larvae from a) the field, 1971 (N = 1160) and b) the basin, 1979 (N = 1833).

Table 4. The number of capelin larvae caught per cubic meter in the basin at 1 m, 2 m and 3 m depth at 0900, 1500 and 2400 hours during the experimental period. 4 C = four-chamber net, 2 C = two-chamber net.

Net	Age in days	Hours								
		0900			1500			2400		
		1 m	2 m	3 m	1 m	2 m	3 m	1 m	2 m	3 m
	5							0	12.8	12.0
	6				2.1		5.8			
	7	0		14.1						
	8							31.0		24.0
4 C	9	1.7		17.4	0.4		11.2			
	10				0.4		24.0			
	11				0.8		8.7			
	12	2.1	24.4	7.0	0.8	1.6	3.7	40.9	36.0	9.5
	15	2.1		5.4						
	16	31,2	19.1	15.3	0.3	23.1	21.1	32.9	16.3	47.3
	20	0,7	8.3	33.2	0.7	7.9	86.5	1.3	115.2	27.5
	23	1,1	10.8	10.0	0.1	2.8	9.7	0.1	31.7	19.1
	26	0.3	16.1	40.5	0	2.4	12.7	8.5	56.3	21.7
	29	0	1.6	8.8	0	1.1	3.1	8.1	52.4	5.9
	33	0	1.1	2.8	0	0.8	0.5	0	33.7	20.0
	35							0	30.7	17.1
	40	0.1	0.8	0.3	0	0.3	0.7	0	16.0	7.6
	41	0	0.5	0.4	0	0.3	0.7			
	43	0	0	0.4	0	0	0.1	0	3.2	6.8
	47	0	0.1	2.8	0	0.1	0.8	0.3	7.5	3.7
	50	0	0	2.4	0	0	0.4	0	7.1	4.5
2 C	53							0	0.1	0
	54							0.3	4.1	25.6
	57				0	0	0	0.1	7.7	4.0
	61							0.1	0.4	1.6
	64							0.1	8.4	18.5
	68							0	1.6	4.1
	71							0	0	4.1
	75							0.1	1.9	8.0
	78							0	7.9	9.5
	82							0	1.2	9.5
	85							0.3	4.7	4.1
	92							0	0	2.4
	96							0.1	1.5	10.3
	99							0.3	0.3	7.5
	115							0.3	0.3	14.5
	117							0	0.3	4.1

Table 5. Number of capelin larvae caught per cubic meter in horizontal hauls 1. June (age 16 days) at 0900 hours with two-chamber (2 C) and four-chamber (4 C) nets at 1 m, 2 m and 3 m depth in the basin.

Net	Filtrated volume in m^3	1 m	2 m	3 m
4 C	2.4	1.2	13.6	9.5
2 C	7.5	31.2	19.1	15.3

first 15 days when they were taken in small numbers of all depths. Table 5 gives the number of larvae caught per cubic meter at 0900 hour and ages 16 days of the larvae, with the two different nets used. It indicates, as do Table 4 and Fig. 10, that there was a great variation in the number of larvae caught per cubic meter with two nets and with the same net throughout the experimental period.

The calculated standing crop of capelin larvae in 1, 2 and 3 m depths, corresponding to 76.5% of the total volume of the basin, are shown in Fig. 11. The curve is established from samples at 24 hours. The figure indicates a reduction of 35% in the number of larvae within the first 20 days. The standing crop curve indicates a great decrease in the population of capelin larvae in the period from 20 to 40 days, with a daily mortality rate of 10.4%. During the rest of the experimental period, the daily mortality rate was 1.4%. At day 40, 7% of the capelin larvae were still alive, and 2.1% survived until the end of the experiment.

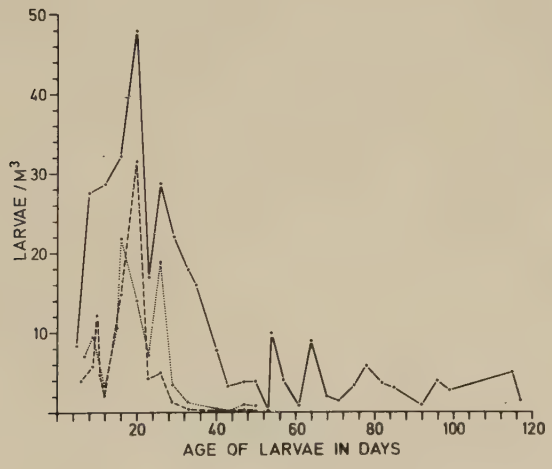

Fig. 10. The mean number of capelin larvae per cubic meter caught within 1, 2 and 3 m depths in the basin at 0900 (.....), 1500 (– – –) and 2400 (———) hours.

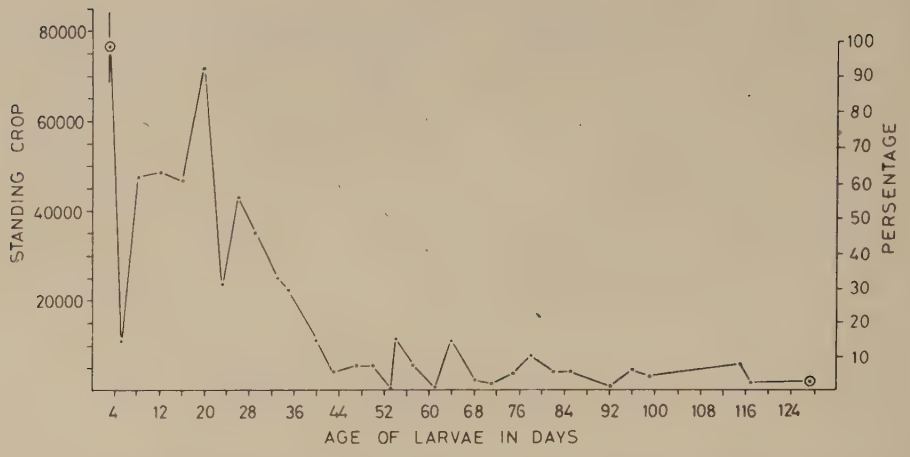

Fig. 11. Calculated standing crop of capelin larvae in 1, 2 and 3 m depths in the basin during the experimental period. ○ = The start and end point. Vertical bar = standard deviation.

DISCUSSION

FEEDING INITIATION

Fish larvae usually start feeding before yolk exhaustion. The capelin larvae started to feed at age 4 days at 8°C in the laboratory. Field observations showed that the larvae started to feed at the same development stage and at a lower temperature in the sea, indicating that the larvae were older than 4 days. This is in contrast to the suggestion of FRIDGEIRSSON (1976) that the capelin larvae could start to feed just after hatching. Gut contents in capelin larvae with large yolk sacs were observed by BJØRKE (1976) but he did not calculate the yolk sac volume. This may be the reason for the difference between his results and the present ones.

FOOD UPTAKE

The observed gut content (2–3 food items per larvae) in the laboratory experiment with fed animals did not result in any growth of the capelin larvae after EYS. The capelin larvae in the basin experiment grew fastest shortly after EYS. The larvae from the basin and the field surveys had a gut content (1–2 food items per larvae) below what was observed in the laboratory. As the growth of larvae in the basin was higher shortly after EYS than in the laboratory experiment, the observed values of the gut content in the basin and the filed are assumed to be underestimated, probably due to defecation of the gut contents during capture and fixation.

From age 20 to 64 days the larvae fed mostly upon larvae of *Spionidae* spp., which were dominant in the basin at that time, and upon innumerable

unidentified matter. This made it impossible to calculate the food uptake of the capelin larvae at this stage. Unidentified matter was also dominant in the gut of sea-caught capelin larvae. After the decrease in the density of larvae of *Spionidae* spp. in the basin, the capelin larvae changed their diet to veligers of *Littorina* spp., which became the dominant species in the zooplankton community in the basin. At the time the larvae of *Spionidae* spp. became important prey organisms for the capelin larvae, the capelin larvae were large enough to eat most of them. The results indicate that the capelin larvae prey upon the dominant organisms of suitable size in their surroundings. The vertical distribution of the capelin larvae and their prey organisms indicated that the distribution of capelin larvae depended on light and temperature and not on the distribution of prey organisms. However, the vertical movement of the prey was not investigated.

GROWTH

Capelin larvae in the laboratory and the basin experiment were observed to reach EYS at age 10 days (8°C). Because of lower temperatures in the sea (3–8°C), the EYS stage for sea-caught larvae occurred some days later (16 days at 2°C), as shown by Helgesen (1977).

The capelin larvae in the laboratory experiments showed retardation in growth at the EYS which coincided with observations made by Helgesen (1977). The capelin larvae in the basin experiment, however, had their maximum mean growth in length during the 12 first days (0.29 mm/day). A similar maximum increase in length for the first 20 days has earlier been observed for autumn spawning herring larvae by Gamble *et al.* (in press).

Growth rates, both in length and weight, are expected to be determined by the density of zooplankton as confirmed by another basin experiment with capelin larvae (Øiestad and Moksness 1977). In that experiment two groups of capelin larvae were given prey densities more than 10 times higher than observed in this investigation. Their growth in length was 0.44 and 0.31 mm/day in the first 26 and 15 days, respectively.

The observed growth rates for capelin larvae in the basin experiment are within the calculated values (0.11–0.38 mm/day) for sea-caught capelin larvae from Canadian waters (Jacquaz, Able and Leggett 1977).

SURVIVAL

The number of capelin larvae caught in the basin experiment showed a great variance both with particular net and with time throughout the experimental period. The reason for the low number of larvae caught during the first 12 days of the basin experiment might be a low rate of dispersion from the area along the walls where the larvae were released. The larvae are expected to be almost evenly distributed in the basin at day 12. From age 15 days, most of the larvae were found below the 2 m-deep thermocline. Sampling below 3 m depth was impossible. However, the volume below 3 m corresponded to only 6% of

the total volume in the basin, and few capelin larvae are expected to be located in this part of the basin during the night.

The negligible mortality in the starving groups in the laboratory up to the end of the yolk sac stage (EYS) indicates a small mortality during the yolk sac stage also for the larvae in the basin. HELGESEN (1977) observed a daily mortality rate of 1–4% at this stage in the laboratory. Using a 1–4% mortality for the first 20 days of the basin experiment gives an estimated standing crop in 1, 2 and 3 m depths between 35,000 and 63,000 capelin larvae. This is in accordance with the calculated standing crop based on sampled larvae in the basin. A higher mortality rate (10.4%/day) was observed from 20 to 40 days of age, resulting in a 58% decrease in capelin larvae in the basin. This was more than 6 days later, and lasted longer than the mass mortality of the starving larvae in the laboratory.

The low feeding incidence (10%) of the capelin larvae in the basin up to age 20 days might be due to total defecation of the gut contents on capture and concentration, but this seems unlikely. The increase in feeding incidence observed during the mass mortality (day 20–40) in the basin support the assumption that most of the 10% of larvae with food in their guts previously belonged to the 7% of capelin larvae surviving until day 40. After day 40 the smallest larvae disappeared from the net hauls which might indicate that most of them did not get enough food during the first feeding stage to continue growth after EYS, resulting in death during the mass mortality period.

The observed feeding incidence (6%), up to a length of 13 mm, of the capelin larvae from the sea indicate that a similar mass mortality due to starvation may take place there. However, the number of sea-caught larvae longer than 13 mm are too small to conclude that a similar mass mortality due to starvation took place in the sea.

The results of the experiments on capelin larvae in the basin and on larvae from the surveys indicate that this mass mortality occurred at the same developmental stages, but the sea-larvae were older due to lower temperatures. These results are in accordance with findings on larvae of other fish species. Basin experiments with cod larvae (ELLERTSEN *et al.* in press) showed a heavy mortality among the smallest cod larvae after EYS, and similar delays and prolongations of the mass mortality period were observed among herring larvae in a plastic bag experiment by SCHNACK (in press) and in the sea by DRAGESUND and NAKKEN (1973).

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PRIMARY GROWTH INCREMENTS IN OTOLITHS OF COD LARVAE (*GADUS MORHUA* L.) OF THE ARCTO-NORWEGIAN COD STOCK

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ABSTRACT

GJØSÆTER, H. and TILSETH, S. 1982. Primary growth in otoliths of cod larvae (*Gadus morhua* L.) of the Arcto-Norwegian cod stock. *Fisk.Dir. Skr. Ser. HavUnders.*, *17*: 287–295.

Primary growth increments have been detected in the otoliths of wild-caught, first-feeding cod larvae, living in a habitat where the light intensity is above the light threshold for visual feeding during 24 hours, and where the larvae were observed to have captured prey organisms both day and night. The comparison of increment counts and estimated age based on larval morphological characters, indicate a daily periodicity of the increments, but the relationship between the variates is not very strong in the very early larval stages.

INTRODUCTION

In recent years the primary growth increments in the otoliths have been used to age several larval fish species. The daily nature of these growth increments has been verified in larvae reared in the laboratory (BROTHERS, MATHEWS and LASKER 1976, TAUBERT and COBLE 1977, BARKMAN 1978, RADTKE 1980, RADTKE and WAIWOOD 1980) and in the field (LIEW 1974, STRUHSAKER and UCHIYAMA 1976, SCHMIDT and FABRIZIO 1980, WILSON and LARKIN 1980).

RADTKE and WAIWOOD (1980) showed that the primary growth increments in laboratory-reared cod larvae of age one to six days were formed daily. This was also found in cod larvae hatched in the laboratory and reared in a large outdoor basin in southern Norway for 35 days (GJØSÆTER 1981).

The mechanisms by which these increments are laid down is believed to be dependent on an internal diurnal clock which has to be entrained by outher cyclic stimuli (TAUBERT and COBLE 1977). However, while these authors suggest a 24 hours light/dark cycle to be essential, BROTHERS (1979) found that primary growth increments could be formed under constant light conditions under a cycle of rise and fall in temperature. Another factor which could be responsible for the periodic growth of the otoliths is a cyclic diurnal food intake.

It is known that cod larvae are visual feeders, with a lower light intensity threshold for feeding at 0.1–0.4 lux (Ellertsen *et al.* 1980). Due to the high latitude of the principal spawning ground of the Arcto-Norwegian cod stock, the Lofoten area, the larvae will experience an extended light period upon hatching.

The present paper presents the results of an investigation of the otolith formation in first-feeding cod larvae sampled in the Lofoten area during the first 14 days of May, after the majority of the larvae had hatched.

MATERIALS AND METHODS

Cod larvae were collected on the spawning grounds in Lofoten (Northern Norway) during a cruise from 3 to 15 May 1980. The larvae were sampled by a Juday net (80 cm, 180μm mesh size) hauled from 30–0 m. During 24 hours on 13 to 14 May larvae were sampled by a submersible electric pump (Flygt B 2125, capacity 3.5 m^3/min.) at 5, 10, 15, 20, 25, 30 and 35 m depth every second hour. The light intensity was measured during the same 24 hours every hour from the surface to 40 m depth by a Techtronix J 16 photometer (J 6501, Illuminance probe). A subsample of the larvae were placed in 96% ethanol, other samples were conserved in buffered formaline. The pH in this formaline was found to be 8.0 at the time of otolith extraction.

After measuring the larvae to the nearest 0.1 mm standard length, the otoliths were extracted and prepared for inspection in a compound microscope. When possible, all three pairs of otoliths were removed. The larva was placed in a drop of water on a glass slide under 50 X magnification. The dissection was done with fine insect needles mounted on glass rods. The otoliths were washed in 96% ethanol, dried and mounted in Canada balsam. The mounted otoliths were then inspected at 1000 X mangnification and the otolith radii and number of increments were noted.

After otolith extraction the following parameters were noted: Myotom height, gut and swimbladder length, yolk sac stage, stomach and gut content, and filling degree.

The sea temperature had been measured in the Lofoten area during the three weeks preceeding the sampling of cod larvae. Using the above-mentioned larval characteristics and temperature, the larval age was estimated on the basis of the description given in Ellertsen *et al.* (1980). The age was estimated to within two-days intervals.

RESULTS

From two to nine primary growth increments could be counted in the otoliths. The increments are composed of one dark and one light zone, together measuring about 2 μm. In most of the otoliths the zones were relative easy to count, and the variation between repeated counts was low. In some otoliths it

was difficult or impossible to detect any increments. Some of these otoliths were more or less opaque; in others extremely narrow light and dark rings could be seen faintly, two rings together measuring from 0.5 to 0.75 μm. It is unknown whether these are real zones in the otoliths or just «optical rings» caused by lens abberation or light diffraction in the aragonite crystals. These rings are not counted as primary growth increments in this study.

Of the 44 larvae initially examined, four could not be aged due to damaged yolk sac remains, five could only be aged «greater than 12 days», and another five had unreadable otoliths.

Table 1 summerizes the data associated with the cod larvae used for increment determination, averaged over the intervals used for the estimation of age from larval characteristics.

Table 1. Data associated with the cod larvae used for increment determinations.

Number of larvae	Estimated age (days)	Number of growth increments		Mean larval length (mm)	Mean otolith radius (μm)
		Mean	Range		
3	3–5	2.3	2–3	4.5	14
1	5–7	2.1	–	4.5	16
14	7–9	3.6	2–9	4.3	19
7	9–10	5.4	3–8	4.7	19
5	9–12	5.6	5–6	4.7	20

Fig. 1 shows the sagitta from a 5.1 mm larva, where nine increments can be seen, of which number three and four are thicker and more distinct than the others.

There is a positive correlation between standard larval length and number of growth increments ($r=0.27$) (Fig. 2). The variation is large and increases with increasing number of increments. Although there is considerable variation, there is a positive correlation between the number of increments and estimated age (Fig. 3). A functional regression (RICKER 1973) was fitted to the pairs of variates. The resulting regression line,

$$N = -4.68 + 1.04 \times A$$

where N is the number of growth increments in the otoliths, and A is the estimated age in days of the larvae, is drawn in Fig. 3. The number of pairs of variates is 30, and the correlation coefficient $r = 0.62$. This regression line transects the «age-axis» at 4.5. days. Its 95% confidence interval is $0.77<b<1.41$.

Fig. 1. Sagitta from a 5.1 mm cod larvae, 800 x magnified in a light microscope.

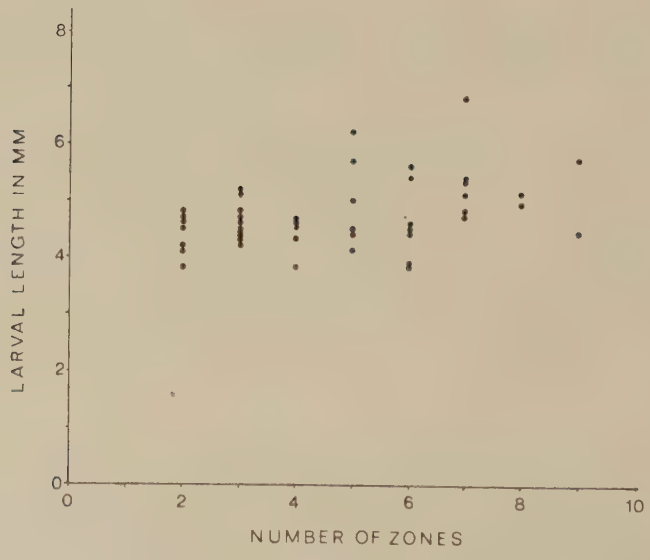

Fig. 2. Standard larval length plotted against number of otolith growth zones.

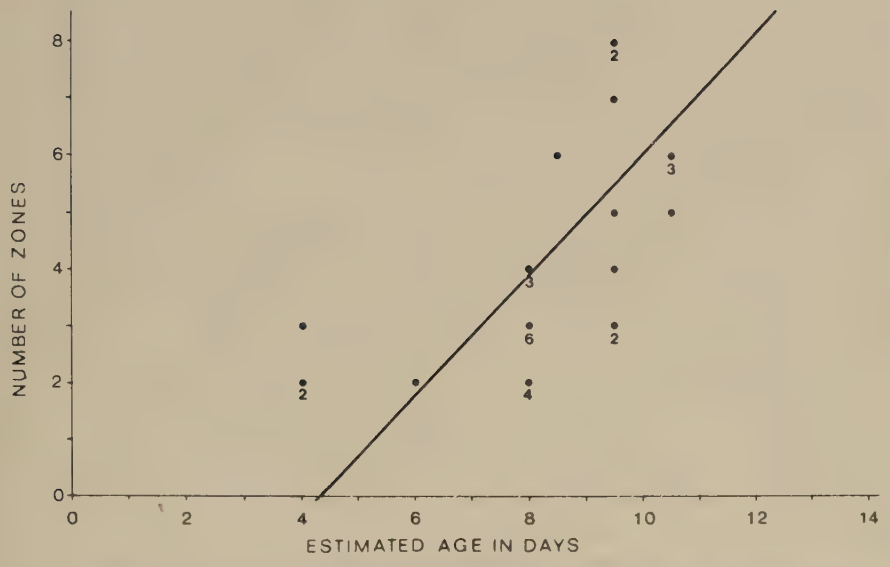

Fig 3. Number of otolith growth zones plotted against estimated larval age. The line drawn is the functional regression presented in the text.

The vertical distribution of cod larvae during 24 hours on 13 to 14 May in the Austnesfjord, Lofoten, is presented in Fig. 4. There was no tendency to diurnal vertical migration, and the maximum consentration of cod larvae was found between 10–25 m depth.

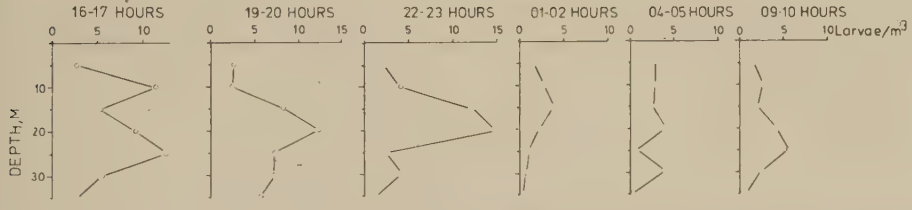

Fig. 4. The vertical distribution (larvae/m^3) of cod larvae in the upper 35 meters during 24 hours on 13. to 14. May 1980 in the central part of Austnesfjord, Lofoten, Norway.

Fig. 5 shows the variation in light intensity from the surface to 40 m depth during 24 hours on the same day and at the same locality. The lowest light intensity was observed at 0100 hours when the light intensity was about 10 lux just below the surface and 0.1 lux at about 38 m depth.

The results of the larval gut content analysis from the same 24 hour-station are presented in Table 2. The percentage of larvae with gut content (mainly copepod nauplii) was 91 to 100% from 1600 h to midnight. At midnight the feeding incidence dropped to between 50 and 45%, and increased to 86% at 1000 hours. However, larvae with undigested nauplii in the gut were observed

at all hours, showing that the larvae had been able to capture prey organisms within the last 15 to 30 minutes prior to sampling (dissolution rate of copepod nauplii in the gut of first feeding cod larvae has been observed to take 15 to 30 minutes at 5°C; TILSETH unpublished data).

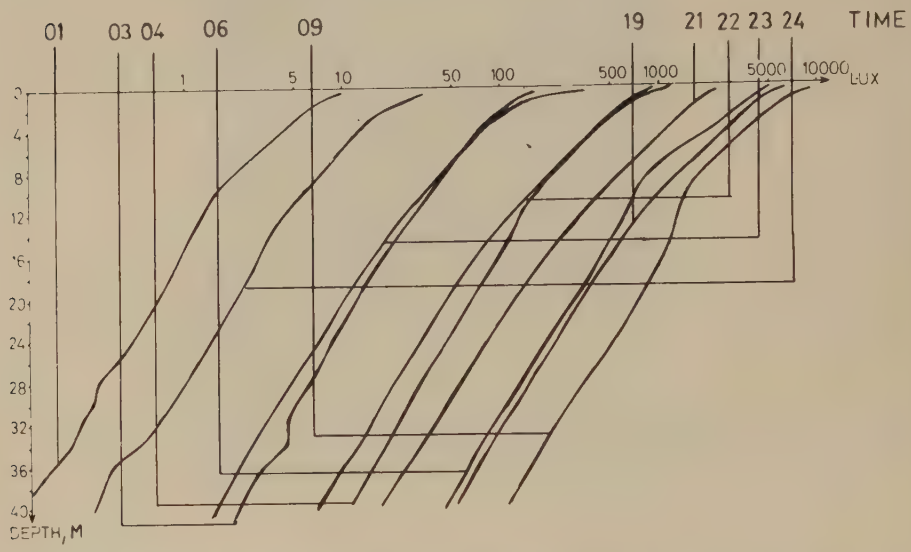

Fig. 5. The variation in light intensity in the upper 40 meters on 13. to 14. May in the central part of Austnesfjord, Lofoten, Norway (N 68°19.0', E 14°44,5').

Table 2. The feeding incidence (FI;% larvae with gut content) and the percentage of larvae with newly captured nauplii (NC) in the gut sampled during 24 hours at different depths on 13. to 14. May 1980 in Austnesfjorden, Lofoten, Norway.

Date	Hours	Depth	NC	FI	Number of larvae
13/5	1610	10 m	24	100	22
»	1650	25 »	23	95	21
»	1940	20 »	17	91	22
»	2000	30 »	20	91	22
»	2230	20 »	9	95	22
14/5	0100	20 »	16	50	21
»	0120	20 »	5	45	22
»	0430	20 »	6	70	20
»	0725	20 »	5	95	22
»	1010	25 »	5	86	22

DISCUSSION

The otoliths had a dark nucleus (in transmitted light) with a diameter of about 10 μm. The increments are laid down concentrically around the nucleus, normally with one or two broader dark zones with a diameter of about 20 to 25 μm. On some otoliths 4–5 increments could be seen between these more distinct zones and the nucleus; on others, one or two could be counted.

Of the 44 larvae examined, only 5 were discarded due to unreadable otoliths. The readability was, however, often different between the otoliths of the same larva. The sagitta was the easiest pair to read, probably mostly due to the larger size, and only this pair was used for increment determination of the larvae. The counts of the other pairs were compared to these, and no systematic difference was found between the pairs. This result is tentative because the set of otoliths was complete only in a few cases. There was also sometimes noted a different readability between the two sagittae. This is believed to be caused by the plan-convex form of these otoliths. The increments are best seen when the plane side lies upwards, but unfortunately, the otoliths, which are placed on the slide in an unpredictable way, can hardly be handled due to their small sizes.

The linear regression drawn on Fig. 3 shows that the number of increments are proportional to estimated age with a proportionality factor close to 1.0. This indicates a daily periodicity of these increments. The regression line transects the «Age axis» between estimated age 4 to 5 days post hatching. This means that the first otolith primary increment is deposited 4 to 5 days post hatching, which coincides with the time of first exogenous feeding when the jaw apparatus becomes functional, described by Ellertsen *et al.* (1980).

Based on these results, Fig. 2 can be viewed as a plot of length versus age, where the age is estimated by the number of increments plus four days. Both the shape and variation of this relationship is typical for larval groups of cod raised in the laboratory (Ellertsen *et al.* 1980). This fact cannot be taken as proof for the validity of ageing by means of primary growth increments. It indicates, however, that length measurement alone cannot be used as an ageing method for the early stages of field-sampled larvae.

The light measurement in the depth strata where the larvae were found (Fig. 5) showed that the larvae never experienced light intensity levels below 0.1–0.4 lux which was found by Ellertsen *et al.* (1980) to be the light intensity threshold for feeding. The results from the stomach content analysis (Tables 1 and 2) show that food particles were found in the majority of the larvae both day and night. The data in Table 2 seem to indicate a diurnal cyclic feeding activity. However, the data are based on samples from only one 24 hours-cycle. Ellertsen *et al.* (1976) found two peaks with high feeding incidence in first-feeding cod larvae during 24 hours-sampling stations in the beginning of May at the same locality in 1976, and in 1977 they found no variation in feeding incidence during 24 hours (Ellertsen *et al.*, unpublished data). It is reasonable to believe, when observing newly captured prey organisms in the gut of first-feeding cod larvae at all hours during 24 hours, that the variation in

feeding incidence was due to variations in the accessibility of prey organisms during that particular 24 hours sampling station (Fig. 4; see also TILSETH and ELLERTSEN 1981).

Although the cyclic variation in the light intensity level does not automatically induce a cyclic feeding activity as long as the light intensity never falls below the threshold of 0.1–0.4 lux, it may, however, act as a timing stimulus for the larvae, and thereby act as a trigger function. As there are no data on otolith growth patterns from 1976 and 1977, it is at present impossible to assess which factor could be the ultimate cause of the observed otolith growth pattern.

The observed variation in the relation between number of growth increments and larval age estimated from morphological criteria may be due to several causes.

Two types of methodological errors may be present. There can be errors in the estimated larval ages. This source of error is probably small as the stages from hatching to yolk sac stage 7 (which is the end of the yolk sac stage) can be identified fairly well. As the temperature regime experienced by the larvae is known, it is possible, on the basis of laboratory experiments, to age these stages with fairly high accuracy. Errors in the counting of the increments may have induced some variability. This source of variance is also probably small for good otoliths, but can be substantial for those with a low readability. However, some larvae may have failed to lay down an increment each day, or they may not have started the increment formation at exactly the same age. The causes of this variability and its effects on the ageing method based on larval otolith reading, is at present uncertain.

Ageing by means of otolith primary growth increments has proved to apply for several species and environments. This preliminary study of cod in an arctic or cold temperature area indicates that this method may in the future also be applied to the Arcto-Norwegian cod stock and other stocks inhabiting similar regions.

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